Minireview

Memory systems of the brain: A brief history and current perspective

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Abstract

The idea that memory is composed of distinct systems has a long history but became a topic of experimental inquiry only after the middle of the 20th century. Beginning about 1980, evidence from normal subjects, amnesic patients, and experimental animals converged on the view that a fundamental distinction could be drawn between a kind of memory that is accessible to conscious recollection and another kind that is not. Subsequent work shifted thinking beyond dichotomies to a view, grounded in biology, that memory is composed of multiple separate systems supported, for example, by the hippocampus and related structures, the amygdala, the neostriatum, and the cerebellum. This article traces the development of these ideas and provides a current perspective on how these brain systems operate to support behavior.
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The idea that memory is not a single faculty of the mind is not itself new. One can find expressions of this idea in the writings of psychologists and philosophers more than a century ago. For example, it is often noted that Maine de Biran wrote in 1804 about mechanical memory, sensitive memory, and representative memory (Maine de Biran, 1804/1929), and that William James (1890) wrote separate chapters on memory and habit in his *Principles of Psychology*. Another percipient writer was Bergson (1910). Focusing on habits, he wrote:

[It is] a memory profoundly different ... always bent upon action, seated in the present and looking only to the future... In truth it no longer *represents* our past to us, it *acts* it; and if it still deserves the name of memory, it is not because it conserves bygone images, but because it prolongs their useful effect into the present moment. (p. 93).

One can identify other antecedents as well. McDougall (1923) distinguished between explicit and implicit recognition, and Tolman (1948) wrote at length on the proposition that there is more than one kind of learning. Most often in the earlier literature, one finds this idea expressed as a dichotomy between two kinds of memory. Thus, Ryle (1949) distinguished between knowing how and knowing that, and Bruner (1969) contrasted memory without record and memory with record. In the 1970s a similar distinction was discussed in the artificial intelligence literature as procedural and declarative knowledge (Winograd, 1975).

Yet these writings did not lead to a single view of the matter. What was finally needed was not philosophical discourse or psychological intuition but experimental inquiry into how the brain actually stores information. The modern experimental era arguably began when Milner (1962) demonstrated that a hand–eye coordination skill (mirror drawing) could be learned over a period of days by the severely amnesic patient H.M. in the absence of any memory of having practiced the task before. While this finding showed that memory was not

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unitary, discussions at the time tended to set aside motor skills as a special case that represented a less cognitive form of memory. The idea was that all the rest of memory is of one piece and that all the rest of memory is impaired in patients like H.M.

Subsequently, and into the 1970s, there were two strands of work that moved the focus beyond motor skills. One strand came from studies of experimental animals, and the other strand came from work with amnesic patients. In the case of animal studies, distinctions were drawn between recognition and associative memory (Gaffan, 1974), contextual retrieval and habit (Hirsh, 1974), and taxon and locale memory (O'Keefe & Nadel, 1978). These proposals had in common the idea that the hippocampus, and perhaps related structures, was involved in one particular type of memory. Yet, the proposals also differed from each other and their prescience was not widely appreciated, in part because at the time the findings in experimental animals did not conform well to the findings from human memory and amnesia. Indeed, one of the reasons that it took a long time to develop an animal model of human amnesia was that it was not understood what needed to be modeled. That is, the description of human amnesia was itself incomplete, and many tasks given to experimental animals were in fact tasks that animals could succeed at just as patients succeeded at motor skills.

However, after an animal model of human amnesia was established in the nonhuman primate (Mishkin, 1982; Squire & Zola-Morgan, 1983), a useful correspondence was established between the findings for experimental animals and humans, and since that time work with experimental animals has been invaluable for understanding the memory systems of the brain.

The second strand of relevant work in the 1960s and 1970s came from demonstrations of unexpectedly good learning and retention by amnesic patients on tasks other than motor skill tasks (Milner, Corkin, & Teuber, 1968; Warrington & Weiskrantz, 1968). However, there were two reasons why these findings, and others that followed in the subsequent few years, did not lead to proposals of multiple memory systems. First, even when the performance of amnesic patients was good, it sometimes fell short of normal levels. Second, in those cases when amnesic patients did perform normally, or near normally, a dominant view was that amnesia was therefore a retrieval deficit (Warrington & Weiskrantz, 1970, 1978; Weiskrantz, 1978).

Quite apart from issues of interpretation, it took some time to appreciate the crucial role of test instructions in determining whether amnesic patients performed as well as controls. For example, amnesic patients often performed well when they were given three-letter word stems as cues for previously presented words, a demonstration of what would later be termed priming. Only later was it appreciated that normal performance by amnesic patients depended on a nonmemory kind of instruction (Use this word stem to form the first word that comes to mind). With conventional memory instructions (Use this word stem as a cue to retrieve a previously presented word), controls performed better than amnesic patients (Graf, Squire, & Mandler, 1984).

The fact that amnesic patients do perform normally when these tests are structured appropriately (for an early example, see Jacoby & Witherspoon, 1982) showed that the phenomenon of priming is a distinct form of memory, separate from what is impaired in amnesia (Schacter & Buckner, 1998; Tulving & Schacter, 1990). Evidence for the special status of priming also came from studies of normal subjects (Tulving, Schacter, & Stark, 1982). These authors wrote "... we are tempted to think that [these priming effects] reflect the operation of some other, as yet little understood, memory system." (p. 341). Perhaps the most compelling evidence for the independence of priming and the kind of memory impaired in amnesia came much later from parallel studies of perceptual priming (Hamann & Squire, 1997; Stark & Squire, 2000) and conceptual priming (Levy, Stark, & Squire, in press). This work showed that severely amnesic patients can exhibit fully intact priming while performing at chance on conventional recognition memory tests for the same test items.

During the period that priming was discovered to be intact in amnesia, it also became appreciated that motor skills are not special after all but are a subset of a larger domain of skill-like abilities, all of which are preserved in amnesia. The first example was the task of mirror reading, a perceptual skill, which amnesic patients acquired at a normal rate despite poor memory for the words that they read (Cohen & Squire, 1980). Other demonstrations followed (e.g., the ability to resolve stereoscopic images, Benzing & Squire, 1989; cognitive skill learning, Squire & Frambach, 1990; artificial grammar learning, Knowlton, Ramus, & Squire, 1992; and category learning, Knowlton & Squire, 1993).

Initially, these data were interpreted according to a distinction between declarative and procedure knowledge (Cohen & Squire, 1980). Other, similar dichotomies also came into use [e.g., explicit and implicit memory (Graf & Schacter, 1985); memory and habit (Mishkin, Malamut, & Bachevalier, 1984)]. However, during the 1980s, it became progressively difficult to fit the accumulating data to the two poles of a dichotomy. For example, emerging findings about priming led Tulving and his colleagues to write:

But even if we accept the broad division of memory into procedural and propositional forms and the division of propositional forms into episodic and semantic forms, there are phenomena that do not seem to fit readily into such a taxonomy. (Tulving et al., 1982, p. 336).

Work with experimental animals also influenced the movement away from dichotomies. First, in the early 1980s, the cerebellum was discovered to be essential for delay eyeblink conditioning (McCormick, Clark, Lavond, & Thompson, 1982), a form of learning that was entirely preserved both in animals with hippocampal lesions (Schmaltz & Theios, 1972) and in severely amnesic patients (Clark & Squire, 1998; Gabrieli, McGlinchey-Berroth, Gluck, Cermak, & Disterhoft, 1995). Second, the neostriatum was identified as important for the sort of gradual, feedback-guided learning that results in habit memory (Mishkin et al., 1984), and an elegant double dissociation was demonstrated in rats after fornix and caudate lesions in two tasks that appeared to measure declarative memory and habit memory, respectively (Packard, Hirsh, & White, 1989). A similar contrast between declarative memory and habit memory was later demonstrated for amnesic patients and patients with Parkinsons's disease (Knowlton, Mangels, & Squire, 1996). Finally, it was shown that still other types of learning, which involve the attachment of positive or negative valence to a stimulus, as in fear conditioning or conditioned place preference, have an essential dependence on the amygdala (Davis, 1992; Fanselow, 1994; LeDoux, 2004; McDonald & White, 1993).

Given the wide variety of learning and memory tasks explored in these studies, and the number of different brain structures that were implicated, an account of memory based on a two-part dichotomy came to appear overly simplistic. Indeed, one wondered what the various kinds of memory that were preserved in amnesic patients had in common aside from the fact that they were not declarative. Accordingly, beginning in the mid 1980s, the perspective shifted to a framework that accommodated multiple (i.e., more than two) memory systems (see for example, Tulving, 1985). At that time, the term "nondeclarative" was introduced with the idea that declarative memory refers to one memory system and that "nondeclarative memory" is an umbrella term referring to several additional memory systems (Squire & Zola-Morgan, 1988). The seminal volume of this period, *The Memory Systems of 1994* (Schacter & Tulving, 1994), presented a collection of writings that largely reflected this point of view.

The result of all this was that it was now possible to reach a clearer, more concrete, and ultimately a more accurate classification of memory by placing the work within a biological framework. Fig. 1 illustrates a taxonomy that incorporates these ideas (for the earliest version of this diagram, see Squire, 1987). Declarative memory is the kind of memory that is meant when the term "memory" is used in everyday language. It refers to the capacity for conscious recollection about facts and events and is the kind of memory that is impaired in amnesia and dependent on structures in the medial temporal lobe and midline diencephalon. Other characteristics of declarative memory allow the term to be extended to experimental animals and bring work with humans and animals into more comfortable contact. Thus, declarative memory allows remembered material to be compared and contrasted. It supports the encoding of memories in terms of relationships among multiple items and events. The stored representations are flexible and can guide performance under a wide range of test conditions. Declarative memory is representational. It provides a way to model the external world, and as a model of the world it is either true or false. In contrast, nondeclarative memory is neither true nor false. It is dispositional and is expressed through performance rather than recollection. Nondeclarative forms of memory occur as modifications within specialized performance sys-
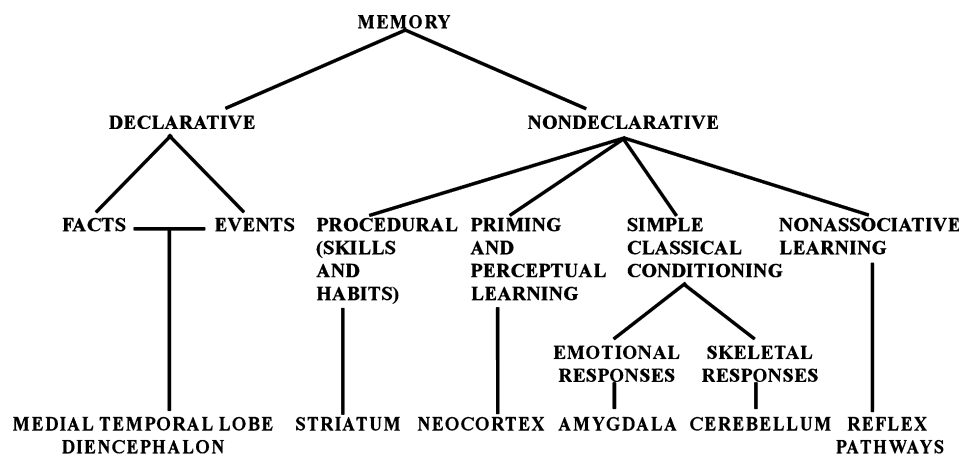

Fig. 1. A taxonomy of mammalian long-term memory systems. The taxonomy lists the brain structures thought to be especially important for each form of declarative and nondeclarative memory. In addition to its central role in emotional learning, the amygdala is able to modulate the strength of both declarative and nondeclarative memory.

tems. The memories are revealed through reactivation of the systems within which the learning originally occurred.

Declarative memory can be divided into semantic memory (facts about the world) and episodic memory (the capacity to re-experience an event in the context in which it originally occurred) (Tulving, 1983). Episodic memory requires the participation of brain systems in addition to those that support semantic memory, for example, the frontal lobes (Shimamura & Squire, 1987; Tulving, 1989). It is an interesting question whether nonhuman animals have a capacity for episodic memory (Tulving, 2002), but the idea is difficult to put to test (for relevant experiment and discussion, see Clayton & Dickinson, 1998; Tulving, in press).

The various memory systems can be distinguished in terms of the different kinds of information they process and the principles by which they operate. In the case of declarative memory, an important principle is the ability to detect and encode what is unique about a single event, which by definition occurs at a particular time and place. In the case of nondeclarative memory, an important principle is the ability to gradually extract the common elements from a series of separate events. Sherry and Schacter (1987) suggested that multiple memory systems evolved because they serve distinct and functionally incompatible purposes. For example, the gradual changes that occur in birdsong learning are fundamentally different from and have a different function than the rapid learning that occurs when a bird caches food for later recovery.

The memory systems of the brain operate in parallel to support behavior. For example, an aversive childhood event involving being knocked down by a large dog can lead to a stable declarative memory for the event itself as well as a long-lasting nondeclarative fear of dogs (a phobia) that is experienced as a personality trait rather than as a memory. The idea that memory systems operate independently and in parallel is nicely illustrated by a study of rats that was carried out in a four-arm, plus-shaped maze (Packard & McGaugh, 1996). First, the upper (north) arm was blocked, and rats were started from the lower (south) arm and trained to turn to the west to find food. Probe trials were introduced at various times by starting rats from the north arm (with the south arm now blocked). In probe trials given early in training, rats entered the rewarded (west) arm, that is, they returned to the place where food had been found. In probe trials introduced later in training, rats went to the nonrewarded arm, that is, they turned east, thereby repeating the left-turn *response* that they had previously made to find food. Place responding early in training was abolished by lidocaine injections into the hippocampus, and rats exhibited no preference for either arm. Correspondingly, later in training, the preference for a left-hand turn was abolished by lidocaine injections into the caudate nucleus. Interestingly,

in this case rats did not behave randomly but now exhibited place responding (that is, they turned west). Thus, even though behavior was dominated later in training by the caudate nucleus, and by left-hand turns, information remained available about the place where food could be found. When the caudate nucleus was disabled, the parallel memory system supported by the hippocampus was revealed.

While one memory system may substitute for another in the sense just described, what is learned differs markedly depending on which memory system is engaged. In the rat, what is learned might be a spatial location or a turning response. In humans, the difference can also be quite striking. For example, consider a task introduced by Tulving, Hayman, & MacDonald (1991), in which simple three-word sentences are presented as novel "facts" to be learned, e.g., *medicine cured hiccups*. In a recent study, sentences were presented repeatedly across several sessions, and recall was subsequently tested by asking participants to complete the first two words of each sentence so as to form a sentence that had been studied (*medicine cured*) (Bayley & Squire, 2002). When the hippocampus and related structures were able to support performance, as in healthy volunteers, learning occurred rapidly and what was learned was accompanied by conscious knowledge about which answers were correct. Further, the learning was readily expressed even if a part of the sentence was replaced by a synonym (*medicine relieved*). By contrast, in severe amnesia, declarative memory was not available and learning was extremely slow. Importantly, what little was learned during 12 weeks of training was outside of awareness, confidence ratings were unrelated to success, and performance succeeded only when the first two words in the test sentences were the same words that had appeared during training.

These findings in humans and rats emphasize that what is important is not only the task that is to be learned but also what strategy is implemented during learning, which in turn reflects what memory system is engaged. Under some circumstances the strategy that is engaged is not optimal for solving a task. For example, hippocampal lesions in rats can *facilitate* the acquisition of a maze task that requires repeated visits to illuminated arms and that is dependent on the caudate nucleus (Packard et al., 1989). The hippocampal lesion presumably disrupts the tendency to use a nonoptimal declarative memory strategy, in the same sense that trying to memorize what one is doing can interfere with human skill learning. Indeed, when humans acquire a difficult habit learning task, structures important for habit learning and structures important for memorizing (i.e., declarative memory) can appear to compete for control of performance. Early in learning, fMRI revealed activity within the medial temporal lobe, as if participants were attempting to memorize the task structure (Poldrack et

al., 2001). As performance improved, activity decreased in the medial temporal lobe and increased in the neostriatum. Activity in these two regions was negatively correlated across participants, consistent with the idea that these regions support different kinds of learning that depend in turn on incompatible learning strategies.

The insight that different strategies can be brought to the same learning problem helps explain the otherwise surprising discovery that some tasks that are learned declaratively by humans are nevertheless learned nondeclaratively by experimental animals. The best-known example of this circumstance is visual pattern discrimination learning (e.g., + vs. →). Monkeys with large medial temporal lobe lesions are intact at the learning and retention of pattern discriminations (Squire & Zola-Morgan, 1983). Yet, amnesic patients learn such tasks in a few trials, like normal individuals, and then later forget which stimulus is the correct one (Squire, Zola-Morgan, & Chen, 1988). The difference appears to lie in the fact that monkeys learn the pattern discrimination task gradually during several hundred trials in a manner reminiscent of skill learning (Iversen, 1976) and that humans approach the task as a simple problem of memorization. Whereas in humans the learning and retention of pattern discriminations is dependent on the medial temporal lobe, in monkeys the pattern discrimination task is dependent on an inferior temporal lobe-neostriatal pathway (Mishkin et al., 1984; Teng, Stefanacci, Squire, & Zola, 2000). To achieve a two-choice discrimination task for humans that is acquired as a skill, and in the way that monkeys learn the pattern discrimination task, one might ask humans to learn to discriminate between the paintings of a master and the paintings of a talented forger.

The notion of multiple memory systems is now widely accepted (Eichenbaum & Cohen, 2001; Schacter, Wagner, & Buckner, 2000; Squire, Stark, & Clark, 2004). Yet it is interesting that one can still find the exclusively psychological perspective "... that there is only one memory system, which preserves all experiences and is used in all tasks" (Whittlesea & Price, 2001). Similar viewpoints have been advanced occasionally during the past 20 years. Typically, the notion is that there is only one memory system but that there are multiple processes operating on this system or multiple ways of accessing its contents. The difficulty with such views is that they are unnecessarily abstract and make insufficient contact with biology. For example, the findings from eyeblink conditioning provide direct evidence for a kind of memory that can be acquired, stored, and retrieved in the absence of the forebrain. Other kinds of memory (e.g., perceptual learning, declarative memory) do require the forebrain. The locus of memory storage is entirely different in these cases, and the learning proceeds by different principles. Perhaps there is some level of abstraction at which synaptic changes within the cerebellum and synaptic changes within the neocortex can be viewed as different expressions of a single memory system. However, such a perspective tends to ignore rather than to embrace the enormous amount that has been learned about neuroanatomy, the molecular and cellular biology of synaptic change, and the organization of brain systems.

In biology, the term "system" is defined in terms of both structure and function. The study of memory has benefited in recent years as discussion of memory systems has drawn increasingly on what is known about biological systems. Strictly functional constructs founded in psychological science alone are seldom sufficient because psychology has matured to the point where it is able to connect concepts about memory to biology. And history shows that, as biological information becomes available about structure and mechanism, explanation becomes more concrete and less dependent on terminology.

During the past two centuries, the study of memory, and the study of cognition in general, has been central to three disciplines: first philosophy, then psychology, and now biology. One can expect the contributions of biology to the study of memory to become even more central in the coming years as more is learned about the molecular biology of synaptic change and the neuroscience of brain systems.

Acknowledgments

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